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## MANZANITA CHAPARRAL IN THE SANTA ANA MOUNTAINS, CALIFORNIA

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A quantitative study of *Arctostaphylos glandulosa* Eastw. chaparral associations in the Santa Ana Mountains was undertaken during the years 1962 and 1963. This phytosociological study correlates numerical data with information on climate, soils, slope exposure, and elevation to estimate the stability, site preferences, and species associations for *Arctostaphylos glandulosa*.

Little consideration has been given to the quantitative aspects of chaparral associations dominated by *Arctostaphylos* species. Major attention has been given to *Adenostoma fasciculatum* H. & A. chaparral, a more widespread and lower elevation community. Extensive studies of *Arctostaphylos* chaparral have possibly been neglected because it is more restricted than *Adenostoma* chaparral, occurs at higher elevations which are often more difficult to reach, and is usually considered impenetrable. Since *Arctostaphylos* chaparral generally occurs at higher elevations, it does not present as many erosion, watershed, or fire problems and is considered of less economic, agricultural, or wildlife importance than chaparral types bordering grazing land, cultivation, or settlement.

The classic work of Cooper (1922) in central California is a floristic study of California chaparral (Delting, 1961). Cooper observed and commented on slope, exposure preferences, behavioral characteristics, humus accumulation, and evaporation ratios of *Arctostaphylos* associations as compared with other chaparral associations. Cooper cited 19 species of *Arctostaphylos* as components of chaparral and classified *Arctostaphylos* site requirements as intermediate between *Adenostoma fasciculatum* and coniferous forest.

Following Cooper's work, a number of studies were made of chaparral ecology, again mainly in *Adenostoma* communities. These include reports by Bauer (1936), Miller (1944; 1947), Sampson (1944), and Wells (1962). Sampson quantitatively studied chaparral succession in central and northern California. He indicated that pine suffered when associated with *Arctostaphylos* due to the greater potential of *Arctostaphylos* to recover after fire by resprouting or by seed germination. Some *Arcto-*

*staphylos* species survive fire by possessing fire-resistant basal burls while other species rely entirely on seeds that depend upon high temperatures for germination (Jepson, 1916). More recently, Wells (1962) correlated mosaic chaparral patterns with geological mosaics and disturbances around San Luis Obispo, California. He noted that the *Arctostaphylos* species *A. obispoensis* Eastw., *A. rudis* Jeps. & Wiesel., and *A. morroensis* Wiesel. & Schreib. had definite soil preferences for serpentine and unconsolidated siliceous sand and succeeded on soils where other plants were unable to survive.

Specific reference to the chaparral in the Santa Ana Mountains was made by Pequegnat (1951) who noted the plant species present, plant-animal associations, and weather conditions in the area. Three *Arctostaphylos* species are listed as present; *A. glauca* Lindl., *A. glandulosa*, and *A. pringlei* Parry var. *drupacea* Parry. He reported that *Garrya flavescescens* Wats., *G. fremontii* Torr., and *A. glandulosa* form an association above 4000 ft elevations.

Abrams (1951), McMinn (1939), and Wieslander and Schreiber (1939) have presented taxonomic descriptions of *Arctostaphylos*. These descriptions define the distribution of species and give clues to possible site preferences.

#### THE STUDY AREA

The Santa Ana Mountains are located in the southern California Peninsular Ranges, a complex of inland and coastal ranges, which extend through Riverside, Orange, and San Diego counties (Jahn, 1954). The Santa Anas are located 10 miles east of the City of Santa Ana, and are about 40 miles long extending southeasterly from the Santa Ana River. The entire range covers approximately 400 square miles varying in width from 4 to 13 miles. The crest with an average height of 3500 ft, is located some 20 to 25 miles from and parallel to the Pacific Ocean. Santiago Peak is the highest point (5860 ft) and Modjeska Peak is the only peak over 5000 ft in the Santa Ana chain.

The Santa Ana Mountains were elevated along the Great Elsinore Fault during the Pleistocene Period. The range has been broken into secondary blocks by further faulting processes, contributing to their rugged character. This range is tilted southwestward with the crest lying near the eastern limits. The east face is a battered fault scarp, drained by short streams. Santiago Creek is the main stream draining the mountains to the west (Hinds, 1952).

Pequegnat (1951) reports that the basement core is partly metamorphosed sediments and granitic intrusives. Along the north and south edges of the range, the ends of the basement core are surrounded by a complex of sedimentary clays, shales, and sandstones.

Close proximity to the sea moderates any climatic extremes in this winter-wet, summer-dry region. Pequegnat (1951) reports that 90% of the precipitation occurs from December to April. Snowfall is moder-

ate with the 3500 ft level as its lower limit. Most precipitation occurs within a belt between the elevations of 2000 and 4000 ft. Fog is common on the Pacific coast slopes in the spring and early summer. The prevailing winds that emanate from the southwest and west are interrupted only by hot, dry "Santa Ana", föehn winds which occasionally sweep down from the high desert.

The vegetational composition is as varied as the undulating topography. Major forms include coniferous forest of *Pseudotsuga macrocarpa* (Vasey) Mayr. and *Pinus coulteri* D. Don., and chaparral. The main vegetational type is chaparral, dominated by *Adenostoma fasciculatum* at lower elevations and by *Arctostaphylos glandulosa* at higher elevations.

The sample stands for this study were scattered over a 12 mile range within the boundaries of the Cleveland National Forest in the central part of the Santa Ana Mountains, and confined to areas of *Arctostaphylos* chaparral. The U.S. Forest Service, Santa Ana Ranger Station fire records show numerous fires for the Santa Ana Mountains since 1922, but fire disturbance has been absent from the study areas for at least 25 years.

#### METHODS

Sample sites were selected using the following criteria: 1. a lack of unnatural disturbances such as bulldozing, road building, and cutting, 2. no natural catastrophe such as fire within the last 25 years, 3. relatively homogenous areas of vegetation, 4. each site uniform in its elevation, slope, exposure, and soils, and, 5. a presence of mature, reproducing plants on established sites. Specimens of all species were collected and classed according to Munz (1959).

Each site was sampled quantitatively with a 100 ft line-intercept and a one-fortieth acre quadrat. The total number of feet intercepting the line was recorded for each species, including overlapping species. From this, relative per cent cover on the 100 ft line was calculated.

Each one-fortieth acre quadrat was placed adjacent to the line-intercept in a rectangle,  $100 \times 10.9$  ft. This quadrat was broken into four contiguous sections each  $25 \times 10.9$  ft. The number of individuals of each species was counted in each quadrat. An individual plant was any plant possessing a burl or trunk distinct from other burls or trunks. Relative per cent frequency, relative per cent dominance, and density of individuals per acre were calculated from the quadrat data. Values of relative per cent cover, relative per cent density, and relative per cent frequency were totaled to obtain importance values (I.V.) (Bray and Curtis, 1957). I.V.'s were derived for each species in each stand. Stands with similar floristic contents, as reflected by species I.V.'s, were classed together in association groups.

Additional measurements included height and number of stems per *Arctostaphylos* individual, elevation, exposure, degree of slope, and soil horizon depths. These measurements, in addition to observations on dis-

TABLE 1. AVERAGE IMPORTANCE VALUES (I.V.) FOR THE SPECIES IN EACH ARCTOSTAPHYLOS ASSOCIATION

Species	Association Groups Oak Manzanita	Manzanita Chamise	Manzanita Coulter Pine	"Pure" Manzanita
<i>Garrya fremontii</i>	12			
<i>Lonicera johnstonii</i>	3			
<i>Rhus diversiloba</i>	13			
<i>Rhus ovata</i>	4			
<i>Rhus laurina</i>	0.4			
<i>Ribes indecorum</i>	9			
<i>Prunus ilicifolia</i>		0.1		
<i>Yucca whipplei</i>		5		
<i>Pinus coulteri</i>			63	
<i>Cercocarpus betuloides</i>	15		1	
<i>Quercus dumosa, wislizenii</i>	153	3	3	
<i>Heteromeles arbutifolia</i>	2	2		4
<i>Adenostoma fasciculatum</i>	14	104	20	24
<i>Arctostaphylos glandulosa</i>	113	174	200	265
<i>Ceanothus crassifolius, leucodermis, tomentosus</i>	7	13	12	8

turbance, fire, growth habits, climate, and other meteorological data (Pequegnat, 1951), were used to determine factors influencing the distributions of plant species and associations.

The data were further analyzed by a mathematical summary which utilizes a coefficient of similarity (Bray and Curtis, 1957). With this coefficient, I.V.'s of the species from each stand were compared to those in all of the other stand sampled. In this way, stands were arranged according to their similarity or dissimilarity in species composition.

## RESULTS

The results obtained are based on the data summarized from 40 one-fortieth acre quadrats and 40 one-hundred ft line-intercepts.

Importance values (I.V.) were obtained for each species. These are summarized in Table 1 for stands classified into four *Arctostaphylos* chaparral associations. The associations; oak-manzanita, manzanita-chamise, manzanita-Coulter pine, and "pure" manzanita are named for the two leading plant dominants. Manzanita stands dominated only by *Arctostaphylos glandulosa* were called "pure" manzanita, since they were practically pure stands.

Table 1 lists the relative importance of each species in its association group and serves as a species presence list.

The two oak species in the oak-manzanita association are *Quercus dumosa* Nutt. and *Q. wislizenii* A. DC. This association group is the most heterogeneous in composition with 13 species represented. When compared to the two dominants, *Quercus* and *Arctostaphylos*, the other species are of minor importance. Among the minor species are *Cercocarpus betuloides* Nutt., *Adenostoma fasciculatum*, *Rhus diversiloba* T. & G., and *Garrya fremontii* Torr.



TABLE 2. AVERAGE NUMBER OF INDIVIDUALS PER ACRE OF THE IMPORTANT SPECIES IN EACH ARCTOSTAPHYLOS ASSOCIATION

Species	Association Groups			
	Oak Manzanita	Manzanita Chamise	Manzanita Coulter Pine	"Pure" Manzanita
<i>Garrya fremontii</i>	160			
<i>Lonicera johnstonii</i>	20			
<i>Rhus diversiloba</i>	80			
<i>Rhus ovata</i>	16			
<i>Rhus laurina</i>	4			
<i>Yucca whipplei</i>		7		
<i>Pinus coulteri</i>			320	
<i>Cercocarpus betuloides</i>	80		6	
<i>Quercus dumosa, wislizenii</i>	1040	3	19	
<i>Heteromeles arbutifolia</i>	4	2		28
<i>Adenostoma fasciculatum</i>	16	1308	24	160
<i>Arctostaphylos glandulosa</i>	800	2142	2443	3520
<i>Ceanothus crassifolius,</i> <i>leucodermis, tomentosus</i>	12	255	118	28
Totals	2232	3717	2,330	3736

In the manzanita-chamise association, few other species are present other than occasional individuals of *Ceanothus* spp. (including *C. crassifolius* Torr., *C. leucodermis* Greene, and *C. tomentosus* var. *olivaceus* Jeps.), and *Yucca whipplei* Torr. This association is the most xeric and occupies the lowest elevations studied.

The manzanita-Coulter pine association is dominated by *Arctostaphylos glandulosa* followed to a lesser extent by *Pinus coulteri* and *Adenostoma fasciculatum*. Again, a few individuals of *Ceanothus* are present.

The "pure" manzanita association is represented by the lowest number of species (four). The *Arctostaphylos* I.V. is high when compared with those of the other three species, of which *Adenostoma* is the most common.

The I.V.'s of *Arctostaphylos* increase as it is associated with *Quercus*, *Adenostoma*, *Pinus coulteri*, and "pure" stands respectively.

The number of individuals per acre for each species is summarized in Table 2 for the four associations. The total number of individuals of all species per acre ranges from 2232 in oak-manzanita to 3736 in "pure" manzanita. Manzanita-chamise and "pure" manzanita have approximately the same total number of individuals per acre. The density of *Arctostaphylos*, like the I.V.'s, increases as it is associated with *Quercus*, *Adenostoma*, *Pinus coulteri*, and "pure" stands. When the average number of stems per *Arctostaphylos glandulosa* individual (five) is multiplied by the number of *A. glandulosa* individuals per acre for each association, the range is from 4,000 stems per acre in oak-manzanita to 17,610 stems per acre in "pure" manzanita. The numbers per acre among the codominants is higher for *Quercus* in the oak-manzanita than it is for *Arctostaphylos*. With the exception of *Adenostoma* in the manzanita-chamise association, the other codominants are low when compared to *Arcto-*

TABLE 3. AVERAGE ABSOLUTE PER CENT COVER FOR THE SPECIES IN EACH ARCTOSTAPHYLOS ASSOCIATION

Species	Association Groups			
	Oak Manzanita	Manzanita Chamise	Manzanita Coulter Pine	"Pure" Manzanita
<i>Garrya fremontii</i>	3			
<i>Lonicera johnstonii</i>	0.3			
<i>Rhus diversiloba</i>	2			
<i>Rhus ovata</i>	2			
<i>Rhus laurina</i>	0.4			
<i>Ribes indecorum</i>	1			
<i>Prunus ilicifolia</i>		0.1		
<i>Yucca whipplei</i>		0.1		
<i>Pinus coulteri</i>			17	
<i>Cercocarpus betuloides</i>	7		0.1	
<i>Quercus dumosa, wislizenii</i>	59	2	1	
<i>Heteromeles arbutifolia</i>		0.4		
<i>Adenostoma fasciculatum</i>		30	3	4.6
<i>Arctostaphylos glandulosa</i>	26	67	80	94
<i>Ceanothus crassifolius,</i> <i>leucodermis, tomentosus</i>	1	3	2	0.6
Bare ground	6.6	5.7	9.3	2.6

*staphylos*. Subdominant species such as *Ceanothus* attained their greatest density in manzanita-chamise stands and to a lesser degree in manzanita-Coulter pine stands. *Garrya fremontii*, another minor species, was fairly dense in the oak-manzanita association.

Table 3 is a summary of absolute per cent cover for the species in the four associations. This is calculated by dividing the total feet of cover (intercept on the 100 ft line) for each individual by the total length of the transect taken and is expressed as per cent. Absolute per cent cover can be used as an indicator of dominance for each species. These figures are proportionately comparable to the density and I.V. data. An additional figure is the per cent bare ground or percentage of the transect devoid of plant cover. The manzanita-Coulter pine association has the greatest percentage of bare ground and the "pure" manzanita association has the least with a 94% cover of *Arctostaphylos glandulosa* and a 2.6% intercept of bare ground. The bare ground figures for all four associations are low (less than 10%) verifying that plant growth is dense in all four associations.

The 40 stands, each designated as an association, were arranged graphically on a target diagram to summarize and compare slope and exposure data (fig. 1). The preferences for slope show that *Arctostaphylos glandulosa* formed solid stands on gentle slopes ( $10-30^{\circ}$ ), mixed with *Adenostoma fasciculatum* on a wide variety of slopes, and occurred with *Pinus coulteri* on steep slopes ( $28-35^{\circ}$ ). *Quercus* species and *Pinus coulteri* locate most successfully on the steeper slopes ( $30-40^{\circ}$ ) (figs. 2 and 3).

Slope is related to soil depth and the presence of organic matter. The gentle slopes of "pure" manzanita had the deepest and richest soils, the intermediate slopes of manzanita-chamise had shallow soils often lacking

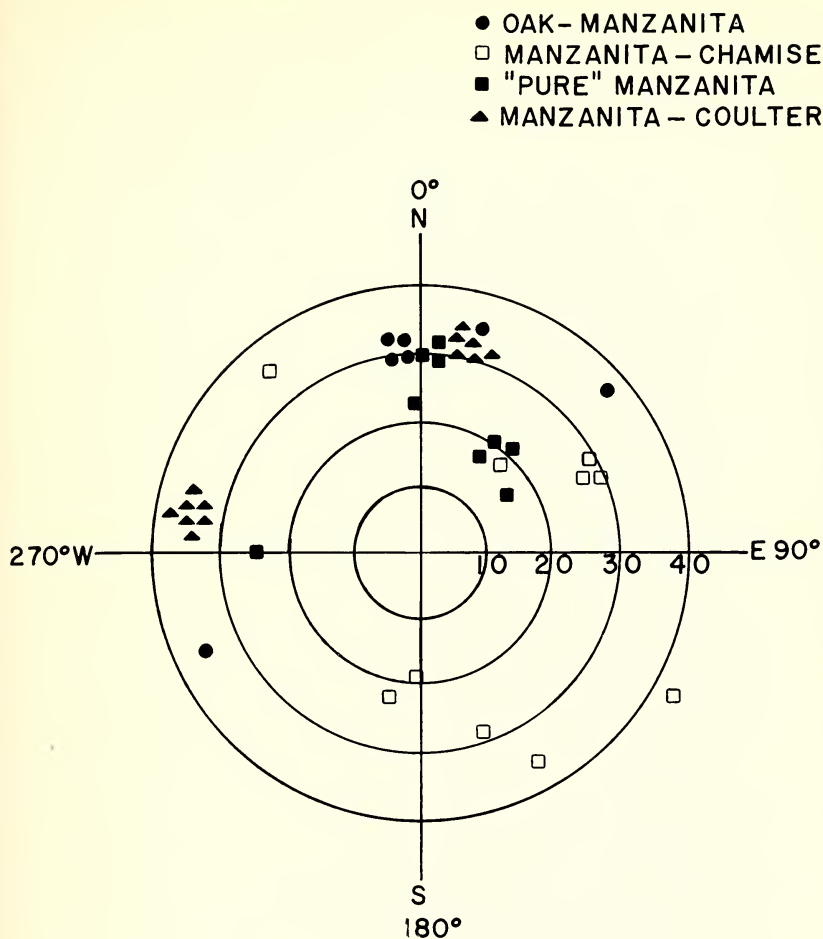


FIG. 1. Slopes and exposures of *Arctostaphylos* association stands. Each circle represents 10 degrees of slope with the smallest circle representing 0-10 degree slopes. Compass directions indicate exposure.

in organic matter, and the steep slopes of manzanita-pine had a general absence of soils.

A gradient of vegetation often follows an elevational gradient, but in the Santa Ana Range, this gradient is highly modified by exposure. Considering exposure preferences, "pure" manzanita was most often located on the north and northeasterly-facing slopes. Manzanita-pine and oak-manzanita were also found on north-facing slopes. Manzanita-chamise was scattered on both north and south-facing slopes, but occurred as the dominant cover on the southerly faces on the seaward side of the main divide. The west faces are warm-xeric with chamise going to the moun-

tain crest. On the colder north exposures, *Adenostoma* does not succeed to the top but generally terminates in a chamise-manzanita association. The east or inland faces support *Cercocarpus betuloides* and *Quercus* species which form a solid cover mixing with *Arctostaphylos* only at the crest.

Stands situated on southwesterly slopes were generally on decomposed granite (quartzite and potash feldspar), while northerly and easterly slope stands were usually on a sedimentary complex of shale and fine clay.

In each plant association depths of soil horizons were measured. Litter ( $A_0$ ) of oak-manzanita stands averaged 1 inch in depth which is less than in any other association. This may be due to a rapid rate of decomposition since the humus layer ( $A_1$ ) averages 6 inches in depth. Chamise-manzanita stands had an average  $A_0$  of 1.5 inches. Slow decay resulted in a shallow average  $A_1$  of 0.6 inches. These stands are on drier slopes with *Adenostoma* providing little cover or soil protection. Pine-manzanita stands had an average  $A_0$  depth of 2.5 inches and an  $A_1$  of 1.5 inches. "Pure" manzanita stands produced the deepest average  $A_0$  of 3.7 inches, with a rich average  $A_1$  horizon of 5 inches.

These results suggest that "pure" manzanita produces and accumulates more litter and organic matter than when mixed with *Adenostoma* or *Pinus coulteri*, and produces excellent humus when associated with *Quercus* on moist sites. As a member of broadleaf chaparral *Arctostaphylos* is a good soil producer, especially when compared to needleleaf *Adenostoma*.

*Arctostaphylos glandulosa* assumes different physiognomic characteristics growing under various conditions or associated with different species.

In manzanita-chamise stands *Arctostaphylos glandulosa* grows to a maximum height of about 6 ft. Branches are thin with numerous laterals and dead twigs remaining on the main stems beneath the surface canopy.

In oak-manzanita chaparral the *Quercus* species and *Arctostaphylos* do not mix but grow as separate aggregations (fig. 3). In other respects the growth character of *A. glandulosa* is much like that in manzanita-chamise stands. Small open areas within *Quercus* clumps are often filled by *Arctostaphylos* suggesting that it can grow in oak litter, but perhaps not in oak shade or deep oak litter.

Beneath *Pinus coulteri*, *Arctostaphylos glandulosa* stems grow prostrate and parallel to the ground. At the edge of the pine canopy, the stems respond phototropically and become vertically orientated. The tallest *A. glandulosa* individuals (14 ft) were measured in this association.

*Arctostaphylos* in pure stands forms a dense mass of branch meshwork (fig. 4). This type of growth produces a uniform canopy. Individuals grow from 10 to 12 ft in height, with stout, twisted stems lacking twigs beneath the canopy.





FIG. 2. A manzanita-Coulter pine association on a northeast slope. *Arctostaphylos glandulosa* occupies the gentler slopes and the *Pinus coulteri* occupies the steeper slopes of the drainage pattern.

In all associations, *Arctostaphylos* stems were observed to grow at right angles to the slope or to exhibit a down-hill tendency.

*Heteromeles arbutifolia* M. Roem., like *Quercus*, grows adjacent to *Arctostaphylos* with few individuals intermixing. Most *H. arbutifolia* plants grow on steeper sites in isolated clusters away from *Arctostaphylos*. The *Ceanothus* species appear to be rapidly declining. Most of the *Ceanothus* plants encountered were either dead or failing. Surviving plants were usually taller than the surrounding *Arctostaphylos* indicating that the shading competition of *Arctostaphylos* may hasten the death of the relative short-lived *Ceanothus*. *Garrya* observed in association with *Arctostaphylos* exhibited growth habits similar to those of *Arctostaphylos*.

Herbaceous plants were generally absent in the understory of *Arctostaphylos glandulosa* chaparral. Annuals, perennials, and grasses were found only on disturbed sites, along road cuts, or on fire breaks in this chaparral.

#### DISCUSSION

For ease of comparison, the community approach categorizes the natural vegetation in the mind of the investigator. In reality, the vegetation is not always as neatly segmented or defined by sharp borders and actually varies gradually and continuously, both in time and space. The vegetation in this study is summarized into four associations. These associations become convenient tools in isolating segments and lumping floristic similarities for the purpose of summarizing trends.

The oak-manzanita association has the greatest variety of species, perhaps because it is found on steep and rocky terrain which provides a great variety of environmental conditions and thus a number of ecological niches.

In comparing the role of competition between *Pinus coulteri* and *Arctostaphylos glandulosa* it appears as though *P. coulteri* cannot successfully compete with the fire-resprouting *A. glandulosa* in the face of repeated burning. After fire *P. coulteri* establishes itself in rivulets, channels, and erosion patterns where the burls of *A. glandulosa* have been washed out or in areas too steep or unstable for *A. glandulosa* to persist. Manzanita-Coulter pine associations contained little *Adenostoma* and even less *Ceanothus*. The lack of living *Ceanothus* is attributed to the lack of disturbance in the area for at least the last 25 years (Hadley, 1961; Patric and Hanes, 1964). *Ceanothus* is known to be relatively short-lived and to require fire or other disturbances to reproduce (Quick and Quick, 1961). Accounts of competition between *Pinus coulteri* and *Arctostaphylos* species indicate that often with fire, the association may give way to a *Ceanothus-Arctostaphylos* association or "pure" manzanita (Cooper, 1922; Sampson, 1944; Zobel, 1953).

The "pure" manzanita association occupies the most gentle slopes, has the highest number of individuals per acre, and provides the most complete cover (fig. 4). The cover produces a canopy equal to that of a forest (Cooper, 1922) and demonstrates the greatest control of the ground surface.





FIG. 3. A gentle north slope supporting "pure" manzanita. The steeper surrounding slopes were covered mainly with *Quercus dumosa* and *Q. wislizenii*.

The dense, tight growth and closed canopy of *Arctostaphylos glandulosa* have several marked affects on the microenvironment of the stands. Direct soil insolation is prevented and subsequent drying is retarded. Evaporation from the soil surface is reduced producing semi-mesic conditions. The closed canopy tends to eliminate competition of other species as evidenced by the lack of seedlings or herbaceous plants in the understory. Strips of *A. glandulosa*, in which canopy cover was mechanically removed by cutting, contained many shade intolerant

shrub seedlings and herbaceous plants. The umbrella-like canopy affords protection against raindrop compaction and erosion. However, erosion by rain is not as important in the Santa Ana *Arctostaphylos* belt as it may be elsewhere. The major forms of precipitation in this "cold" chaparral are fog-drip, freezing moisture (hoar frost), and snow.

The high density of stems retards slope erosion, aids water infiltration, and adds large quantities of litter in the form of twigs and leaves, thus influencing soil genesis. This litter is not readily washed, wind-blown, or lost by desiccation as it is in *Adenostoma* chaparral. More organic matter is accumulated and retained in *Arctostaphylos* chaparral than in any of the other Santa Ana chaparral types. The mesic nature of the soil aids in rapid decay and incorporation of organic material with mineral soil (by chaparral comparisons), producing a pronounced A<sub>1</sub> soil horizon (Wilson, 1963). *Arctostaphylos glandulosa*, then, is a good soil builder and watershed cover as compared to other chaparral types.

Cooper (1922) noted that *Arctostaphylos* species showed a preference for degree of slope and became established as a dominant on the most gentle slopes available in a favorable site. He also noted that *Arctostaphylos* gave way to oak and pine on steeper slopes. Similarly, *A. glandulosa* in the Santa Ana Mountains formed solid stands on the gentlest north and northeast slopes above 3200 ft elevation in the presence of marine air and grew with *Pinus coulteri* and *Quercus* species on the steeper slopes (fig. 1). Of the steepest slopes (40°–100°), the xeric, unstable types with running tallus were occupied by *Quercus* while the more mesic, stable precipices were covered by *Pseudotsuga macrocarpa*. Occasional *Arctostaphylos* plants grew in rocky crags or on steep cliffs but did not form solid stands. The germination, seedling, and rooting requirements of *Pinus coulteri*, *Pseudotsuga macrocarpa*, and *Quercus* species may enable them to dominate pioneer and unstable sites of steeper slopes, rocky outcrops, or slides. *Pinus coulteri* is also found on gentle slopes but is limited, possibly because it cannot successfully compete with the burl-sprouting *Arctostaphylos glandulosa*. In many areas, *A. glandulosa* with the aid of fire, appears to be a potential successor of pine. Barring disturbance, established *P. coulteri* might gradually replace the apparently long-lived *Arctostaphylos* stage of fire succession. However, succession is complicated by periodic fires and subsequent erosion, as well as by fungus and insect damage or kill to the *P. coulteri* (Pequegnat, 1951). Further research is necessary to determine precisely the relative successional positions of *A. glandulosa* and *P. coulteri*.

The exposure of slope is another important factor which affects the establishment of *Arctostaphylos*. The most dense stands are on north-facing slopes, particularly those slopes reached by the late winter, spring, and early summer fogs. These fogs strike the upper ocean-facing slopes and crests. As they billow over the crest, through openings, and across lower ridges, they afford moisture to some upper and northern slopes not





FIG. 4. The interior of a "pure" manzanita stand with the typical high density of stems and heavy cover of solid *Arctostaphylos glandulosa*.

directly exposed to the sea. In addition, these northern slopes receive less solar insolation. Since the north faces are not directly exposed to the prevailing westerly winds, they are also subjected to less transpiration stress. Coulter pine-manzanita is correlated with the presence of fog belt areas on northern exposures.

East-facing slopes are in a fog and rain shadow and are subjected to descending winds with greater evaporation-transpiration stress for

plants. These east slopes support *Quercus-Cercocarpus* chaparral with only scattered individuals of *Arctostaphylos* near the crest.

Amplitudes of tolerance and successional relationships are implied from the results of the comparisons of similarity and dissimilarity of stands outlined in the Methods. Each species associated with *Arctostaphylos* has its own amplitude of tolerance or range of ecological requirements and no two amplitudes are the same for any of the species. Stands with a predominance of *Quercus* are the most dissimilar from those dominated by *Arctostaphylos*. Therefore, *Quercus* and *Arctostaphylos* are considered the most dissimilar in their ecological requirements. *Arctostaphylos* and *Pinus coulteri* are the most similar. Within the Santa Ana Mountains, *Quercus* species find optimum growth conditions in hot, dry environments while *Arctostaphylos glandulosa* and *Pinus coulteri* prefer cooler and semi-mesic environments. *Adenostoma* differs from *Arctostaphylos* in that it reaches greatest importance on hot, xeric sites exposed to marine air. *Ceanothus*, although suffering from old age, demonstrated the widest amplitude of tolerance of any species in the *Arctostaphylos* chaparral associations, occurring with *Adenostoma*, *Pinus*, and *Quercus*.

All of the species vary gradually and continuously on an elevational gradient. That is, none of the species start or end abruptly at a certain elevation. This gradient is greatly modified by exposure, slope, soils, fire, and air currents. However, optimum conditions as reflected by the greatest numbers are found for *Adenostoma* at lower elevations, and for *Arctostaphylos* and *Pinus* at the highest elevations.

#### SUMMARY

Little quantitative or phytosociological study has been made of *Arctostaphylos* chaparral in the southern California Peninsular Ranges. In this study, it is proposed that *Arctostaphylos glandulosa* is a significant unit in the Santa Ana Mountain "cold" chaparral as; 1. a forest (*Pinus coulteri*) competitor, 2. a potential factor in watershed management, 3. an important contributor in soil genesis, and 4. a possible agent of erosion control.

Importance values derived from the line-intercept and quadrat data are used to classify the 40 stands sampled into four associations; 1. oak-manzanita, 2. manzanita-chamise, 3. manzanita-Coulter pine, and 4. "pure" manzanita. These *Arctostaphylos* associations are designated by dominant and codominant species present and are all found above 3200 ft elevation in the Santa Ana Mountains. The results indicate that *Arctostaphylos*; 1. becomes a significant dominant when associated with *Adenostoma fasciculatum* at upper elevations on south- and west- facing slopes and at lower elevations on north- and northeast- facing slopes, 2. with fire is a potential successor of *Pinus coulteri* on the north and northeast slopes and ridges, 3. is associated with *Quercus* aggregations but demonstrates mutual exclusion, and 4. forms solid stands on gentle north and northeast slopes above 3200 ft in the presence of marine air.

Plant growth is dense in all four associations with less than 10% bare ground in any association.

A comparison of the species composition of the 40 stands suggests that *Quercus* and *Arctostaphylos* are the most dissimilar in ecological tolerance and that *A. glandulosa* and *Pinus coulteri* have similar requirements. *Quercus* species attain their greatest growth and density in hot, dry environments and *Arctostaphylos* and *Pinus coulteri* find optimum conditions in cooler and semi-mesic environments.

Factors of altitude, exposure, slope, fire, and marine air determine the extent to which *Arctostaphylos glandulosa* successfully competes with associated species to become the dominant plant in the "cold" chaparral of the upper elevations in the Santa Ana Mountains.

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## REVIEWS

*Flora Europaea*. Edited by T. G. TUTIN, V. H. HEYWOOD, N. A. BURGESS, D. H. VALENTINE, S. M. WALTERS, and D. A. WEBB. Vol. 1. Lycopodiaceae to Platanaceae, xxxii + 464 pp., 5 maps. Cambridge Univ. Press. 1964. \$16.00.

From the beginning in 1956, the *Flora Europaea* project has been broadly cooperative, highly organized, and based on a premise that much value lies in having a flora completed in the shortest possible time. Volume I, contributed by 51 authors representing 14 nationalities, provides in part the first synthesis of the European flora on a continental scale and, much to the benefit of most American botanists, in a *single* language. The remaining three volumes are planned for publication within the next eight years. The area covered, shown by maps, extends from Spitzbergen to the Azores and eastward through the Mediterranean (including Sicily, Crete, European Turkey, Crimea, and northern shore of Caspian Sea) to the Ural Mountains.

Readers should be able to name to subspecies any fern (or fern ally), conifer, or flowering plant which grows wild in Europe and also those commonly cultivated. The descriptions are brief but adequate and often are followed by a cogent statement regarding variability and relationships to other taxa—a strong feature. Author or editor credit is provided for each generic treatment. Chromosome numbers sensibly are given only if determined from materials of known wild European origin. A check-list of references will be published separately which ought to explain some new reports such as  $2n = 22$  for *Meconopsis cambrica*. Sections, subgenera, and subfamilies appear where appropriate in the text. All families to be treated in the four volumes are keyed in Volume I. The sequence is Englerian except that monocots will come last. Filicopsida are divided into 21 families. Molluginaceae, Tetragoniaceae, and Parnassiaceae will seem strange to Americans. Paeoniaceae follows Ranunculaceae, Fumariaceae is submerged. *Mahonia* is separated from *Berberis*. *Platanus acerifolia* is considered a synonym of *P. hybrida* Brot. *Raphanus raphanistrum* is divided into five subspecies; *Brassica rapa* L. is favored over *B. campestris*, showing that California botanists have something still to learn. Of very minor moment, Capparaceae is conserved over Capparidaceae and the perigynous condition of *Eschscholzia* was overlooked.

The format should satisfy nearly everyone and there are useful dividends such as the list of basic or standard floras of the region, the list of families in Volume I, and the lists of titles of books and periodicals cited in the text. An index to signs, abbreviations, and explanatory notes, as well as a glossary of technical terms and some English-Latin equivalents are printed on blue paper for quick finding. The only suggestion that I dare make is that type species or lectotype species for genera ought to have been indicated at least when a member of the flora.

Many years will pass before the full significance of the *Flora Europaea* project can be known. Undoubtedly many European botanists, besides the contributors, will be stimulated to look once again at the plants in their own backyards. The numerous statements of compromise in this text point out many interesting problems which call for more detailed study. Instead of bringing floristic researches to a close, the *Flora* surely will be the starting point for an entirely new look at the plants of Europe. With this major effort recently completed, the floristic gaps in the northern hemisphere stand almost as a challenge. Here is a model, which ought